16

Macroarthropods

C. A. Edwards

Rothamsted Experimental Station
Harpenden
Hertfordshire
England

I Introduction · 533
II Groups of macroarthropods involved in litter breakdown · 535
  A Isopoda—woodlice · 535
  B Symphyla—symphylids · 536
  C Diplopoda—millipedes · 537
  D Isoptera—termites · 540
  E Diptera—fly larvae · 542
  F Coleoptera—beetles · 543
  G Other groups · 543
III Populations of macroarthropods · 544
  A Isopoda · 544
  B Symphyla · 546
  C Diplopoda · 547
  D Isoptera · 547
  E Diptera and Coleoptera · 547
IV The role of macroarthropods in litter decomposition · 548
  A Isopoda · 548
  B Symphyla · 549
  C Diplopoda · 550
  D Isoptera · 551
  E Diptera and Coleoptera · 551
V Relative importance of macroarthropod groups in litter breakdown · 551
References · 552

I. Introduction

Plant litter ranges from soft and fragile deciduous leaf tissue to tough, undecomposed wood. Soft and delicate plant tissues are usually rapidly decomposed by microbial action, but some of the tougher tree leaves may take several years to break down, and some woody tissues considerably longer than this. The decomposition of such tissues is a complex process involving both the soil fauna and microflora, each acting to facilitate further breakdown by the other.

Soil animals aid in the breakdown of plant organic matter in several ways:

1. By physically disintegrating tissues and increasing the surface area available for bacterial and fungal action.
2. By selectively decomposing material such as sugar, cellulose and even lignin.
3. By transforming plant residues into humic materials.
4. By mixing decomposed organic matter into the upper layer of soil.
5. By forming complex aggregates between organic matter and the mineral fractions of soil.

For several weeks after fresh deciduous litter reaches the forest floor, very little of it is eaten by the fauna, although it becomes invaded by some micro-organisms, especially fungi. During this period the litter darkens, becomes weathered, and water-soluble substances, particularly sugars, organic acids and polyphenols, are leached out. Edwards and Heath (1963) reported that *Fagus* (beech) and *Quercus* (oak) leaves that did not darken appreciably after reaching the soil, began to be fragmented by litter animals much sooner than darker leaves. These darker leaves had a much greater percentage of both polyphenols and sugars than did "shade" leaves (Heath and King, 1964). As the water-soluble polyphenols were removed by weathering, the litter became more palatable to arthropods (Edwards and Heath, 1974). It was suggested that the increase in polyphenolic materials precipitated protein complexes in leaves and made them less digestible by the microfauna (Edwards and Heath, 1963) and King and Heath (1967) confirmed that the amount of polyphenols in beech litter was inversely proportional to the rate at which arthropods consumed the litter (Williams and Gray, Chapter 19).

Satchell and Lowe (1967) studied the palatability of many kinds of leaf litter to the earthworm *Lumbricus terrestris* and reached similar conclusions.

The groups of animals having the greatest influence on the rate of decomposition of leaf litter are earthworms, termites, millipedes, woodlice and larvae of various insects, especially Diptera. The role of earthworms is considered in Chapter 14, and here we are concerned only with the role of macroarthropods. The importance of some of these animals in fragmenting litter has been demonstrated experimentally. When naphthalene was used to minimize the numbers of arthropods in *Quercus* litter, about one twentieth of the litter broke down in 140 days, compared with one tenth when the soil animals were present (Kurcheva, 1960). In similar experiments in U.S.A., 60% of the *Quercus* litter in untreated soil broke down in one year, compared with only 45% in soil treated with naphthalene. When the soil fauna was totally excluded from *Quercus* and *Fagus* litter, by confining it in fine (0·003 mm aperture) mesh bags there was little breakdown, even after 3 years (Edwards and Heath, 1963).

Macroarthropods can also chemically decompose plant material, either by various digestive enzymes or with the aid of symbiotic protozoa and bacteria that live in their intestines. The combined effects of macroarthropod feeding and microbial action are gradually to produce dark, stable humic substances and to decrease the ratio of carbon to nitrogen in the organic matter.

Finally, as most of the organic matter becomes humified, the soil animals mix this material with the mineral soil, and when this process is well advanced in a rich mull soil there are no obvious horizontal strata in the soil profile; instead there is a homogeneous mixture of soil and organic matter.

It is extremely difficult to assess the relative contributions of bacteria and fungi on the one hand, and the micro-, meso- and macrofauna on the other, to the breakdown of plant litter. It seems probable that microbes make a major contribution, and in their absence soil invertebrates would be relatively unimportant. Of the soil animals, the macrofauna seem to play a much more important part than some of the smaller animals. However, all are complementary and have a more or less essential role in breaking down the tougher plant materials.

II. Groups of Macroarthropods Involved in Litter Breakdown

The main groups of macroarthropods that contribute to the breakdown of plant litter are the Isopoda (woodlice), Symphyla (symphylids), Diplopoda (millipedes), Isoptera (termites), Diptera larvae (flies) and Coleoptera larvae and adults (beetles). Small contributions may be made by Psocoptera (booklice), Thysanoptera (soil-inhabiting thrips) and Hemiptera (root-aphids) and even occasionally Trichoptera (terrestrial caddis fly larvae). Of these animals there is little doubt that in temperate countries, millipedes and fly larvae are most important and in tropical areas Isoptera make a major contribution. Each of these groups of animals will be considered in turn.

A. Isopoda—Woodlice

Woodlice are familiar animals usually restricted to sheltered, moist habitats such as plant litter, decaying wood or under stones; they are nocturnal, only emerging from their hiding places at night. They are a terrestrial group of Crustacea, most of which are aquatic, and this relationship means that they are very susceptible to loss of water by evaporation. Woodlice do not hibernate in winter but they remain quiescent for most of this period. They are comparatively long-lived, surviving for as long as 4 years in ideal conditions. Species common in Great Britain in deciduous woodlands are *Trichoniscus pusillus*, *Philoscia muscorum*, *Oniscus asellus* and *Porcellio scaber*.

Woodlice are omnivorous, but feed mainly on dead and decaying plant material, fragmenting this and making it more susceptible to attack by other invertebrates and micro-organisms. They also feed on their own faeces and on those of other animals. Damp leaves and wood are usually preferred, and it is not certain to what extent the leaf tissue must be decomposed by micro-organisms before it becomes acceptable to woodlice. When young, they eat only the softer parts of leaves, but adults of the more robust species eat the whole leaf including veins. As with the soil invertebrates, such as earthworms, woodlice feed much more readily on some species of plant litter than others, and one of the main factors that influence palatability seems to be the sort and amounts of polyphenols in the litter. Leaves that contain large amounts of certain polyphenols, e.g. *Fagus*, are not eaten until the leaves have been weathered and these chemicals broken down or leached out; by contrast, leaves with a low polyphenol content such as *Fraxinus* (ash) and *Acer* (sycamore) are readily eaten soon after they reach the litter layer. Woodlice also seem to feed on decaying wood, but there is no information on the way in which they digest this or how much they break it down. Kühnelt (1961) considered that woodlice play a considerable role in the breakdown of litter and wood residues, but Kevan (1962) concluded that where woodlice are abundant they may be important in the comminution of dead vegetable matter, but cannot be considered to play a major general role in litter breakdown.

B. Symphyla—Symphylids

Symphylids are often considered to be rare animals, but this is more due to their small size and habit of penetrating deep into the subsoil than their actual abundance. They are small, white, active animals with twelve pairs of legs when fully grown. Although they are found in many soils, they are very common in leaf litter and, due to their large numbers and voracious appetites, there is little doubt that they contribute appreciably to the breakdown of plant material. Symphylids are very long-lived, surviving for as long as 10 years in the laboratory. Although all symphylids are polyphagous, eating all sorts of living and dead plant material and micro-organisms, the common species, from the two suborders Scutigerellidae and Scolopendrellidae, differ in their habits. Species from the Scutigerellidae are larger and more active, showing a distinct preference for living plant tissues, whereas those belonging to the Scolopendrellidae tend to feed on decaying plant and animal material or dead micro-organisms. It seems likely that, because of the very rapid throughput of food, e.g. one symphylid can consume 15 times its own weight in a day (Edwards, 1961); there is very little digestion of the food, and their main contribution to litter breakdown is in fragmentation. They seem to prefer the softer leaf tissues, being unable to eat some of the tougher leaves, veins and woody tissues. A fair conclusion would be that although symphylids contribute appreciably to litter breakdown, their role is a relatively minor one.

C. Diplopoda—Millipedes

Millipedes are probably some of the most common of the larger arthropods encountered in forest litter. They are almost exclusively vegetarian or saprophagous, feeding on a great variety of living or dead plant organic matter, although they will also feed on decomposing animal tissues.

They are nocturnal, usually hiding by day and becoming active by night; this is probably due to their susceptibility to desiccation. The litter-inhabiting species include the pill millipedes which roll into a ball when disturbed, the long cylindrical iulid forms which are sometimes called snake millipedes and can actively tunnel into soil, and the flat-back millipedes which are dorso-ventrally flattened and are restricted to the loose litter layers. Millipedes are quite long-lived, some species surviving for several years, and they breed all the year round. They can feed on leaves which have not been otherwise disintegrated (Dunger, 1958; Zachariae, 1965), but usually they feed more readily on weathered leaves (van der Drift, 1951). They eat large quantities of leaf litter, some species of leaves being much more palatable than others. Lyford (1943) reported that the order of decreasing palatability of different species to millipedes, was: *Betula lutea* Mickx. (yellow birch), *Fraxinus americana* L. (ash), *Populus grandidentata* Michx. f. (aspen), *Acer rubrum* (red maple), *Acer saccharum* (sugar maple), *Betula papyrifera* Marsh (paper birch), *Quercus borealis* Michx. f. (red oak) and *Fagus grandifolia* Ehrh. (beech). He believed palatability to be correlated with a high calcium content of the leaves, and Marcuzzi (1970) also agreed that there was some correlation between calcium and palatability. However, it seems much more likely that this order of palatability is a feature of the polyphenol content of the litter, in the same way as is the palatability of leaves to earthworms and woodlice. This idea is supported by observations that *Iulus* and *Cylindroiulus* eat many more beech leaves that have been weathered for a year than those that are newly fallen (van der Drift, 1951), and that oak is preferred to beech (Cloudsley-Thompson, 1951). Striganova (1971) reported that the order of decreasing palatability of four species of leaf litter to millipedes was: *Carpinus*, *Acer*, *Quercus* and *Fagus*. Dunger (1962) gave the order of decreasing preference in the species he studied as: *Tilia* (lime), *Fraxinus* (ash), *Alnus* sp. (black alder), *Ulmus* (elm), *Acer* (maple), *Fagus* (beech), *Quercus* (oak) and red beech, and he also confirmed that weathered leaves were preferred to freshly fallen ones. Although there are marked food preferences, van der Drift (1951) considered that they may not always be clearcut because of a need for a variety of food. It seems probable that availability of food may also influence preferences.

Millipedes can also feed on decaying wood and although it is not clear how they manage to digest this material, they probably do so with the aid of a symbiotic intestinal flora.

There is considerable controversy over the ability of millipedes to break down their food chemically. In experiments on litter from a Dutch beech wood, van der Drift (1951) concluded that there was little difference in chemical composition between the food eaten by *Glomeris marginata* (Villers) and its faeces, and Dunger (1958) reach a similar conclusion. However, Bocock (1963) showed that *Glomeris marginata* could assimilate some holocellulose, soluble carbohydrates and fats. During passage of *Fraxinus* leaf litter through the intestine of this millipede, the percentage of holocellulose fell from 30% to 27%, that of soluble carbohydrates from 4·6 to 4·0% and that of crude fat from 3·6 to 1·7%. These amounts are small, and much more breakdown was reported by Striganova (1971), who found that more than half the cellulose in leaf litter was digested during passage through the intestines of millipedes. Specifically, millipedes consumed 40% of the cellulose in oak and hornbeam litter, 70% of that in beech litter, with an overall daily consumption of 3–5 mg per individual.

Franz and Leitenberger (1948) claimed that the C:N ratio of millipede faeces was greater than that of the litter on which they fed, so that considerable humification occurred during passage through the millipedes' intestine. Dunger (1958) also reported that some humification occurred when millipedes were fed on several kinds of fresh litter that was rich in nitrogen. He obtained similar results with weathered litter of *Fraxinus excelsior* and *Alnus glutinosa*, if it still contained considerable nitrogen. Humification did not occur when millipedes were fed with litter of *Quercus robur*, *Acer platanoides* and *Ulmus carpinifolia*. Bocock (1963) also reported more nitrogen in millipede faeces than in their food (Table I).

In a very careful investigation, Marcuzzi (1970) studied changes in the C:N ratio during digestion by millipedes. The criticism that van der Drift (1951) made of Franz and Leitenberger's work was that humification

TABLE I. Changes in the nitrogen content of *Corylus* litter eaten by *Glomeris*

	Amino Nitrogen (mg g^{-1})	Ammonia Nitrogen (mg g^{-1})	Total Nitrogen (mg g^{-1})
Food	193	175	13,600
Faeces	103	1385	15,700

Adapted from Bocock (1963).

may have occurred microbially, after the faeces had been excreted. Marcuzzi took trouble to eliminate this as a source of error, and found quite marked decreases in the C:N ratio in his experiments (Table II).

TABLE II. Changes in the carbon:nitrogen ratio after passage through the intestines of *Glomeris* spp.

		C:N ratio	
Millipede sp.	Leaf species	Of leaves	Of faeces
(a) *G. euganeorum*	*Castanea sativa*	31·44	20·25
(b) *G. undulata*	*Castanea sativa*	34·48	27·55
(c) *G. conspersa*	*Castanea sativa*	29·82	26·31
(a) *G. euganeorum*	*Fagus sylvatica*	28·50	25·56
(b) *G. undulata*	*Fagus sylvatica*	30·50	26·80
(c) *G. conspersa*	*Fagus sylvatica*	29·86	27·20
(a) *G. euganeorum*	*Quercus ilex*	31·86	27·95
(b) *G. undulata*	*Quercus ilex*	32·10	26·90
(c) *G. conspersa*	*Quercus ilex*	38·79	25·61

Adapted from Marcuzzi (1970).

To summarize the findings of these various workers, it seems that although there is chemical breakdown of the litter and some humification by millipede feeding, by far the most important role millipedes play is in fragmentation and disintegration of large quantities of litter.

Kubiena (1955) emphasized the importance of millipedes in organic matter turnover, when he stated that mull-like moder soil consisted mainly of the droppings of iulid and glomerid millipedes, small earthworms and insect larvae. In an almost pure *Fagus* stand in northern England, Blower (1956) found that the millipedes *Cylindroiulus punctatus* (Leach) and *Proteroiulus fuscus* (Am Stein) were the dominant species of invertebrates, and the soil humus consisted mainly of cylindrical millipede faeces. Similar observations were made in a Dutch beech wood by van der Drift (1951). Eaton (1943) described the formation of a mull soil mainly by a millipede, *Apheloria*, and Jacot (1940) suggested that stocking new forest plantations with millipedes would promote mull formation. Blower (1956), however, concluded that, although mull humus can support large populations of millipedes, there is no evidence that millipedes can produce the clay-humus complex characteristic of mull soils. Lyford (1943) believed that the importance of millipedes in breakdown of litter has been overemphasized, and he concluded that they consumed only 1–5% of the total leaf fall. Bocock (1963) considered that a large population of *Glomeris* would consume 1·7–10% of the annual deciduous litter fall. In complete contrast, Striganova (1971) stated that diplopod activity in some broad-leaved forests of the U.S.S.R. seemed to be the most important factor of leaf litter decomposition. There seems little doubt that millipedes are one of the important elements of the soil fauna in promoting litter breakdown, particularly in temperate regions.

D. Isoptera—Termites

Most species of termites are tropical or sub-tropical, although they sometimes occur in temperate areas. They differ considerably in their habits and food, but all are social insects living in nests or colonies of varying degrees of complexity. They feed almost exclusively on decaying vegetation or wood. In the process of feeding and building their nests, they not only disintegrate plant organic matter, but intimately mix it into the soil. In much the same way as earthworms (see Chapter 14) and millipedes, termites alter the carbon : nitrogen ratio in soil, the ratio being much greater in termite mounts or subterranean colonies than in the surrounding soil.

Thus, termites are very important animals in the breakdown of plant litter and, together with earthworms, they probably contribute more to leaf litter breakdown than all the other soil-inhabiting invertebrates. Termites are one of the few groups of animals that are able to degrade chemically large quantities of cellulose and they rely on cellulose as their main source of energy. Termites have three main types of feeding habit—feeding on leaf litter or humus, feeding on wood or feeding on fungi.

The termite species that are most important in breaking down leaf litter are called foraging termites, and most of these belong to the family Termitidae. They collect freshly fallen or old leaf litter and carry it to their nests, where it is either eaten immediately or stored until required. Although there are distinct preferences by different termite species for particular sorts of plant litter, we have little information on these preferences. There is also some evidence that a particular kind of litter may become either more or less palatable to certain species of termites as it decomposes, just as it does to earthworms. Other species of termites (Hodotermitenae, some Amitermitinae and Nasutiterminae) are called harvesting termites. These tend to prefer to harvest fragments of living plants, especially grasses, which they carry to their nests as food.

Many termites depend upon wood as their source of energy. A few species feed on living wood (Kalotermitidae and Mastotermitidae), but more commonly, they feed on decaying or rotten wood (Kalotermitidae, Rhinotermitidae, Hodotermitidae and some Termitidae) and most prefer wood in advanced stages of decomposition. It is likely that many of the fungi growing on the wood are an important component of the food of termites.

Different species of termites seem to have distinct preferences for decaying wood from particular species of trees, and the preferences are sometimes complex, with certain parts of a tree being preferred to others. It is impossible to assess the relative importance of termites in breaking down particular species of trees. In fact, many species of termites are polyphagous, and eat not only many different kinds of wood, but can also consume plant debris, animal dung, stored products and many other materials.

Termites obtain most of their energy from the digestion of polysaccharides including cellulose and hemicelluloses, and some species can also digest lignin. Four to five times as much cellulose as lignin is decomposed. However, most of this digestion is made possible by symbiotic protozoa and bacteria. Most important are the protozoa found mostly in the hind-gut of termites that can digest not only decaying but also sound wood. Most cellulose digestion is anaerobic, and there is some evidence that the initial product is glucose, which in turn is broken down to carbon dioxide, hydrogen and acetic acid (Hungate, 1943). It is not known how lignin is broken down, but it is probably an aerobic process, although it is not clear how this and anaerobic cellulose breakdown can occur together. Nevertheless, there is good evidence that the rate of decomposition of cellulose and lignin can be quite rapid; in experiments *Kalotermes flavicollis* (Fabricius) decomposed 94–95% of the cellulose, 60–70% of the hemicelluloses and 3–4% of the lignin in the wood upon which it fed (Seifert, 1962).

Some species of termites actually consume large quantities of mineral soil, particularly soil containing much humus (Kalshoven, 1941; Adamson, 1943). Those species that have adopted this habit seem to have modifications of their mouthparts, the grinding ridges of the molar plates being adapted for crushing particles. There is little evidence on how much the humus used as food is decomposed by the termites.

Thus, there is little doubt of the importance of termites in facilitating the breakdown of plant litter. In fact, they are so efficient in this process that they can sometimes decrease the organic carbon content of soil, in situations where the vegetation is comparatively sparse. Harris (1955) considered that termite digestion is so complete that they make only small contributions to soil fertility.

E. Diptera—Fly Larvae

The larvae of Diptera are extremely common in leaf litter and decaying wood. Many different species are found, with a great variety of food preferences. Some feed directly on freshly fallen leaf litter, but the majority of species important in litter breakdown are saprophagous, and feed after there has been some microbial breakdown. Perel *et al.* (1971) stated that in Russia, dipteran larvae are encountered in great numbers in areas ranging from the overmoist taiga forests to dry forests in the forest steppe zone. They studied the role of larvae of Tipulidae in litter breakdown, and found that these larvae would feed on fresh litter and increase its reducibility and ash content. Tipulid larvae can also feed on decomposing litter; they can disintegrate considerable quantities of material. Tipulids are usually much more common in deciduous woodland litter than in that from coniferous forests, and Bornebusch (1930) considered tipulid larvae to contribute the greatest biomass of all Diptera. Chironomid larvae are also very abundant in deciduous leaf litter, particularly in *Fagus* woodlands. Other larvae common in litter are those of the Lonchopteridae and Platypezidae and some Stratiomyidae, all of which are adapted for this habit by their flattened form. Bibionidae larvae are also common in leaf litter and, with the aid of a symbiotic gut flora, can feed on only slightly decomposed leaves as well as well decayed ones. Szabo *et al.* (1966) estimated that the bibionid population in a mixed woodland in Hungary could consume 15% of the total annual leaf fall. Karpachevsky *et al.* (1968) reported that they found evidence of a small degree of humification of litter during passage through the gut of larvae of *Bibio marci*, and d'Aguilar and Bessard (1963) reported a decrease in the C:N ratio of leaves of *Castanea* and *Quercus*, indicating a tendency for humification to occur. Sciarid larvae can also feed on litter in various stages of decay.

Many dipterous larvae feed mainly on fungi; one important group with this habit is the Mycetophilidae and these larvae are very common in decaying wood. Some species such as the larvae of the Sapromyzidae mine in leaf litter. Many of the muscoid fly larvae feed in rotting vegetation, but tend to prefer litter in an advanced stage of decay. Other families which have larvae that feed on various stages of decomposing litter, are the Sciaridae, Borboridae, Trichoceridae, Anisopodidae, Psychodidae and Lonchopteridae.

It seems that fly larvae make a significant contribution to litter breakdown, although less than termites, earthworms and millipedes, but we need much more information on the relative importance of the many different species.

F. Coleoptera—Beetles

A great variety of beetles and their larvae live in forest litter and decaying wood. Many of these, such as the larvae of Clambidae, Corylophidae and Trichopterygidae, feed on decomposing plant material. Some Scaphididae, Cryptophazidae and Lathridiidae feed on micro-organisms and fungi. It is certain that many species of beetle larvae, such as those of Elateridae, live on decomposing leaf litter, but the details of their feeding habits are poorly known, although elaterids are one of the dominant groups of beetle larvae in forest litter. Another very common group of larvae in litter is the Tenebrionidae, many species of which feed on plant remains and living or dead roots. The larvae of some species of Staphylinidae eat decomposing litter as do those of some species of Scarabaeidae.

Many beetles and larvae are wood-feeders but usually, as in the Scarabaeidae and Cerambycidae, they depend on a symbiotic gut flora to digest the cellulose. Not all wood-feeding beetles can digest cellulose; for instance, larvae of the Bostrichidae and Scolytidae and some Staphylinidae merely fragment the tissues. Some species of Elateridae, Ipidae, Tenebrionidae, Buprestidae, Cerophytidae, Throscidae and Eucnemidae also feed on decaying wood, and members of the Scaphidiidae live on fungi that grow on decaying wood.

To summarize, beetles are much less important than fly larvae in the breakdown of leaf litter, but probably more important in the decomposition of decaying wood.

G. Other Groups

Several other groups of macroarthropods contribute to breakdown of plant material. In the Hymenoptera, some species of ants in the Myrmicinae, Dolichoderinae and Formicinae are vegetarian and break down leaf litter. In tropical countries, leaf-cutting ants (Attini) carry large amounts of leaf material to their nests, where it is fragmented and used as a substrate for fungi. However, ants as a group break down a great deal of leaf material.

A few terrestrial species of Trichoptera larvae, e.g. *Enoicyla pusilla* (Burmeister) feed on leaf litter, particularly the underside of *Quercus* leaves.

III. Populations of Macroarthropods

Although populations of macroarthropods vary very considerably between habitats, soil types, species of woodland and climatic region, some groups are clearly more numerous and contribute a greater biomass than others. Figure 1 summarizes some of the data in the classical survey of Danish woodlands by Bornebusch (1930). Diptera larvae were generally the most common but they included a great diversity of types and habits. In functional terms, the Diplopoda are probably much more important.

A. Isopoda

Woodlice aggregate very much in response to environmental conditions, dispersing much more at night. This makes it very difficult to make accurate estimates of populations other than by mark and recapture methods which are relatively inaccurate. As with many other soil arthropods, populations tend to be greater in alkaline conditions than in acid soils (Kühnelt, 1961). This is not surprising when the need for calcium to build their exoskeleton is considered. Woodlice seem to be most characteristic of mull soils, only *Trichoniscus pusillus*, *Oniscus asellus* and *Porcellio scaber* occurring in mor soils. Not all workers agree with this conclusion, and van der Drift (1951) found more woodlice in acid mull (moder) woodland sites than on calcareous mulls in Holland, although he reported that *Armadillidium vulgare* was more common on the alkaline sites. Populations of 250 m^{-2} for *Philoscia* in Britain, 1000 m^{-2} for *Trichoniscus pusillus*, 4000 m^{-2} for woodlice in an Australian forest, 5000 m^{-2} for *Armadillidium vulgare* in California and as many as 7900 m^{-2} for *T. pusillus* in scrub grassland on the Chiltern Hills in Britain have been reported (Sutton, 1972) and large numbers in a British woodland (Table III). These figures are larger than those reported for other woodland species (van der Drift, 1951; Dunger, 1958).

Such populations are rather lower than comparable ones for millipedes and it is generally accepted that isopods are usually less important than millipedes in litter breakdown.

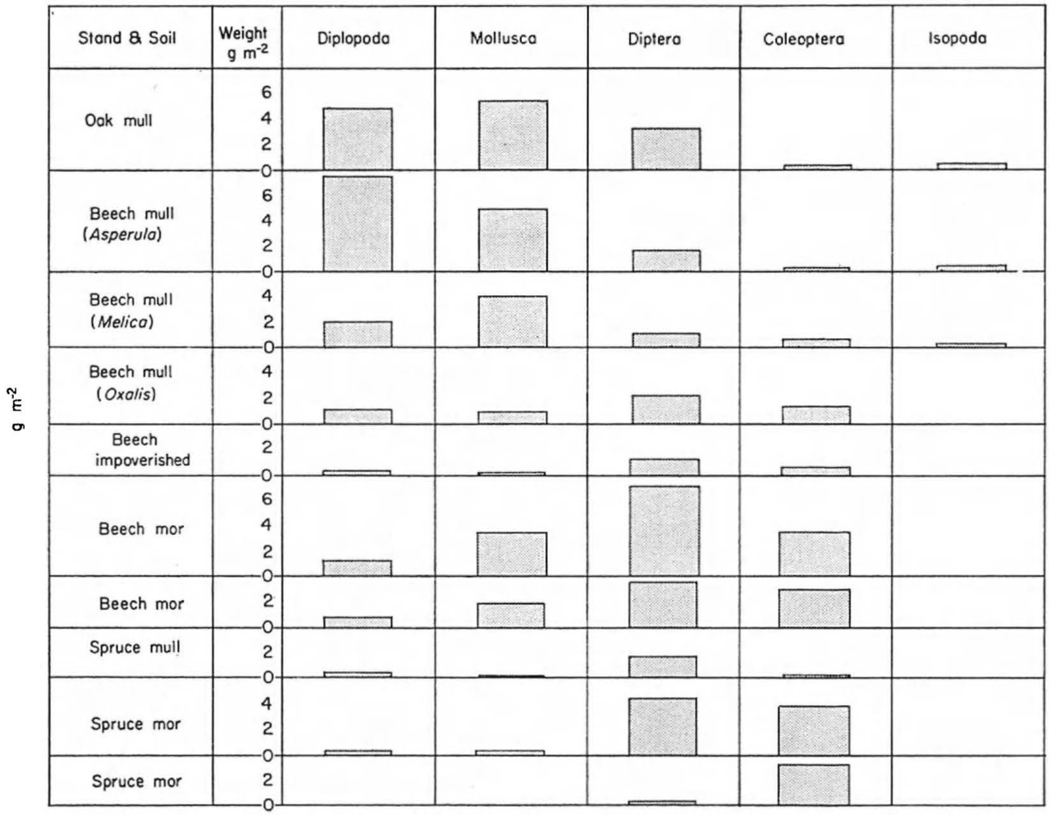

Fig. 1. Biomass of macroarthropods in 10 Danish woodlands (From data by Bornebusch, 1930.)

TABLE III. Numbers and weights of woodlice in grassland in a British wood in March

	Biomass ($g\ m^{-2}$ live wt)	Numbers (no. m^{-2})
Trichoniscus pusillus	1·19	1490
Philoscia muscorum	0·70	103
Armadillidium vulgare	0·21	6
Total woodlice	2·137	1820

Adapted from Sutton (1972).

B. Symphyla

Symphylids are often considered to be rare but in a survey of 415 sites in southern England, Edwards (1958) found that 54% had symphylid populations, and symphylids were found in 26% of all woodland sites.

Because symphylids cannot actively tunnel through soil, but rather move through existing cracks and crevices, they are rather sensitive to the type of soil they inhabit. The soil types that favour build-up of symphylid populations are loams or clay loams, although neither heavy clays nor sandy soils are suitable (Table IV) (Edwards, 1958).

TABLE IV. Populations of symphylids in different soil types (based on 33 sites)

Soil type	Mean number per m^2
Clay	2,100
Clay loam	43,700
Sandy clay loam	59,100
Loam	111,100
Sandy loam	29,600
Sandy	4,800

Data from Edwards (1958).

The largest numbers of symphylids were found in cultivated soils (mean population of 89,700 per m^2), but forest litter also supported large numbers (mean population of 51,520 per m^2) (Edwards, 1958).

C. Diplopoda

Millipedes, like woodlice, are very aggregated, and this makes estimates of populations very difficult. Although soil sampling can be used in grassland, populations in woodlands have to be estimated by methods that depend on activity, such as mark and recapture, pitfall traps or baits. Nevertheless, it is clear that very large populations of millipedes exist in many woodlands.

Millipedes seem to be much more abundant in calcareous soils than in acid ones, and one species, *Cydroiulinlus londiniensis* (Leach), is very sensitive to acidity (Blower, 1956).

Thiele (1956) reported that numbers of *Glomeris marginata* in German woodlands were small, average values ranging from 2·3 to 7·5 per m^2 and Shaw (1968) found populations of *Narceus annularis* (Raf.) of 18·4 per m^2 in a mixed woodland in New York, but Blower (1956) reported at least 70 per m^2 in a sandy woodland soil, van der Drift (1951) estimated populations of 80 individuals of *Cylindroiulus punctatus* per m^2 in a *Fagus* wood, Nef (1957) calculated 110 per m^2 in *Quercus* woodland and Bornebusch (1930) up to 177 per m^2 in Swedish woodlands, and much larger numbers with peak populations of 200–300 per m^2 were estimated by Dunger (1958).

D. Isoptera

Little data are available on termite populations, and there is no exact estimate of the termite population for a particular habitat. Most estimates of the abundance of termites have been made on the basis of the numbers of termite mounds, which are easily counted. Since the numbers of individuals in a colony may range from a few hundred to several million individuals (Lee and Wood, 1971), this is a relatively poor index of abundance. Woodlands tend to have larger numbers of small mounds, rather than fewer large mounds.

There is even less information on the numbers of those species of subterranean termites that do not construct obvious mounds yet are often very abundant. A few of the population estimates that have been made for these species are given in Table V. Some of these estimates are of dubious value, but they do show that in tropical forests termites constitute an appreciable proportion of the soil fauna, and must make a considerable contribution to litter breakdown.

E. Diptera and Coleoptera

The species represented in these two families vary so much in form and habits that overall population estimates are relatively meaningless. Bornebusch's survey of Danish woodlands indicated populations of Diptera ranging from 232 to 1076 per m^2 and of Coleoptera from 44 to 426 per m^2. In view of his methods of extraction these can be considered as underestimates and it would not be unreasonable to expect insect populations of the order of 1000 per m^2. Nef (1957) estimated populations of saprophagous insects as 400–800 per m^2, which agrees with this figure.

TABLE V. Abundance of subterranean termites in various habitats

Habitat	Numbers per m^2	Percentage of total macro-arthropods	References
Rainforests (Panama)	12	0·5	Williams, 1941
Savanna woodland	50	3·0	Lee and Wood, 1971
Semi-arid woodland	69	11·0	Lee and Wood, 1971
Forest (Congo)	500	—	Maldague, 1964
Forests (Trinidad)	2790	34·0	Strickland, 1945
Rainforests (Trinidad)	4450	43·0	Strickland, 1944

Adapted from Lee and Wood (1971).

IV. The Role of Macroarthropods in Litter Decomposition

When data are available for an ecosystem on the energetics and biomass of these groups of animals, it is possible to construct energy budgets and to estimate how much of the total litter fall the animal is consuming and how much it is assimilating. Edwards *et al.* (1970) calculated that large decomposers (macroarthropods, molluscs and earthworms) represented 27–82% of the total invertebrate biomass in soil and contributed 3–33% of the total respiration.

The total litter fall in a stable temperate deciduous forest is about 3·0 t ha^{-1} (ray and Gorham, 1964), which is equivalent to 3000 g m^{-2}. It has been calculated that, for many tree species, earthworms can consume most of this if there is no competition from other animals. If we look at the groups of macroarthropods in turn we can make comparative estimates of their relative contributions to litter breakdown.

A. Isopoda

Woodlice consume a lot more food than they assimilate, although the amount of material assimilated is very variable, ranging from 10 to 70% of the food consumed. It seems probable that much of the variability can be explained on the basis of abundance of food. When food is plentiful it passes through the animal much faster, and much less is assimilated, whereas when there is a shortage it is retained in the gut much longer. When food is abundant, woodlice usually consume much larger amounts (Hubbell *et al.*, 1965). Much of the energy assimilated is used up in metabolism. For instance, *Ligidium japonicum* has been estimated to use more than 80% of the energy it assimilates in this way (Saito, 1965). Saito (1970) reported that the assimilation efficiency of *Armadillidium vulgare* was 0·48, and Phillipson (1966) that the equivalent figure for *Oniscus asellus* was 0·41. Using a figure of 0·45 for *Ligidium japonicum*, Saito calculated that the food consumption of the population in a Japanese evergreen broad-leaf forest was 5·8 kcal m^{-2} year, and such a forest may produce more than 500 kcal m^{-2} year of energy in litter fall.

The total biomass of woodlice in litter is quite small compared with that of some of the other macroarthropods. For instance, Bornebusch (1930) calculated it to be 0–0·28 g m^{-2} in 10 Danish woodlands. With a figure for the average weight per individual of 0·7 mg (Edwards, 1967), and if populations of about 1000 per m^2 are considered to be about average for woodlands, the biomass of woodlice might be expected to be about 7 g m^{-2}; this may be an underestimate, however, because the figure of 0·7 mg was based on small species of woodlice. Hubbell *et al.* (1965) calculated that woodlice eat up to 3% of their body weight per day, so 7 g m^{-2} of woodlice would consume 0·2 g of litter per day or 73 g per year. This is only a very small proportion of the total litter fall.

B. Symphyla

No data for assimilation efficiency of symphylids are available, but Edwards (1961) reported that they could eat up to 15 times their own weight per day. Such a large throughput indicates a very poor assimilation efficiency, particularly since symphylids grow very slowly, often hardly changing in weight for several years.

If an average population estimate for woodlands is 3260 per m^2 (Edwards, 1958), and a figure for the average weight per individual is 0·082 mg (Edwards, 1967), the average biomass would be only about 0·25 g m^{-2}. The rate of food consumption varies greatly with age and moulting phase, but an estimate of 0·05 mg per day per individual is not unreasonable. Using these figures, an average population would consume 0·326 mg of litter per day or 60 g m^{-2} year. This is a rather larger consumption than might be expected, but is probably an overestimate, because symphylids feed on materials other than litter, and at any time a considerable part of the population would be in deeper soil. Obviously they are not of major importance in litter breakdown.

C. Diplopoda

There is considerable variability in the estimates of the amounts of food assimilated by millipedes. van der Drift (1951) claimed that *Glomeris marginata* assimilated only about 6% of the food ingested, Gere (1957) reported assimilations of 3·8–12·4%, and Bocock (1963) of 7·5–10·5%. O'Neill (1968) and Shaw (1970) presented data that showed an assimilation efficiency of about 15%. Striganova (1971) reported that millipedes assimilated 39·4% of the *Carpinus* (hornbeam) litter and 37·6% of the *Quercus* litter that they ate. Franz and Leitenberger (1948) claimed that millipedes could assimilate about 50% of the food they ingest. Gere (1957) reported that millipedes converted 1·7–7·4% of the food they consumed into body tissue, but Bocock (1963) stated that *Glomeris marginata* converted only 0·29–0·45% of the food it consumed into body tissue. His feeding tests showed that this species utilized 6·0–10·5% of the dry matter, 43·2% of the crude fat, 28·4% of the holocellulose, 28·7% of the soluble carbohydrates and 0·3–0·4% of the nitrogen in the *Fraxinus* leaf litter that they ate.

There have been various estimates of the amounts of litter consumed by millipedes. Gere (1957) stated that they consumed 0·5–4·0% of their live weight daily. Striganova (1971) estimated that they ate 3–5 mg of food per individual per day, Gere (1957) found that they ate 0·33–4·1 mg per individual per day with an average of about 2 mg, and Bocock (1963) reported daily intakes of 3·75–11·77 mg per individual.

Populations of millipedes in woodlands differ considerably, but 100 individuals per m^2 can be considered a reasonable average, and with an average biomass of 2·8 mg per individual (Edwards, 1967), the total biomass would be about 0·3 g m^{-2}. This would be valid only for British woodlands, because some species from the U.S.A. and the tropics are very large and weigh several grams when fully grown. Shaw (1968) calculated that the biomass of the population of one of these larger species, *Narceus annularis*, in a mixed woodland in New York State was 2·86 g m^{-2}. If the average daily consumption of litter is assumed to be about 4 mg per individual, a population of 100 millipedes per m^2 would consume about 400 mg or 146 g per year. Striganova (1971) made similar calculations and reached the conclusions that millipedes could consume up to 4800 kg ha^{-1} (480 g m^{-2}) per year of *Quercus*, *Acer* or *Carpinus*. Such a turnover rate would deal with the whole of the annual litter fall at the site quoted, and is almost certainly an over-estimate. Bocock (1963) made more modest claims, estimating that *Glomeris* populations would consume 1·7–10% of the annual deciduous litter fall.

Clearly, millipedes consume large amounts of litter and are one of the most important groups involved in litter breakdown in temperate woodlands.

D. Isoptera

Termite populations per unit area are so poorly known that it is difficult to give an accurate figure for the biomass in tropical woodlands. In a *Brachystegia* forest in the Congo, it was estimated that there was a biomass of 11 g m^{-2} (Maldague, 1964), and in a *Eucalyptus* forest in S. Australia a biomass of 6·0 g m^{-2} was estimated (Lee and Wood, 1971). It seems likely that the range in biomass is of the order of 5–50 g m^{-2} (Lee and Wood, 1971).

The average amounts of food consumed by termites is only poorly known. In feeding experiments, *Kalotermes flavicollis* consumed 2–3% of its body weight (*ca.* 0·2 mg) daily and decomposed 61–62% of this (Seifert, 1962). Lee and Wood (1971) reported that *Nasutitermes exitiosus* (Hill) consumed 0·06 mg per individual per day. They calculated that this represented 16·6% of the total fall of wood or 4·9% of the total litter fall, but the litter fall was small in this woodland.

Maldague (1964) estimated that a termite population in the Congo could consume 570 g plant material m^{-2} year, which represented almost half of the total litter fall, but Lee and Wood (1971) believed this to be an overestimate and suggested that 15% of the total litter fall would be a more realistic figure. Nevertheless, this was only a moderate population and a large population may contribute much more to total litter turnover. Clearly, termites have an important role in the metabolism of woodland ecosystems and in breakdown of plant litter in tropical ecosystems.

E. Diptera and Coleoptera

The populations, habits and food of these animals vary so greatly that it is impossible to make a really valid estimate of their contribution to plant litter breakdown. An average population would consist of about 1000 of these animals per m^2. With an average weight of about 1·5 mg per individual this represents a total biomass of 1·5 g m^{-2}, which is probably an underestimate. If each individual consumes about 0·5 mg of litter per day the amount of litter consumed would be 0·5 g m^{-2} day or a total of 180 g m^{-2} year. This estimate involves a considerable potential error as it takes no account of the variation in habits, size, and type of food of these animals.

V. Relative Importance of Macroarthropod Groups in Litter Breakdown

An estimate of the relative importance of macroarthropods must be extremely approximate in view of variations in numbers and lack of knowledge of the ecology and physiology of these animals (see Käärik, Chapter 5).

Some of the estimates of turnover made in section III are summarized in Table VI.

This summary shows that these animals may consume only about one third of the total litter fall; other groups such as earthworms, bacteria and fungi must therefore account for the rest of the turnover. These data do not account for consumption of faeces by other animals, a common habit of many litter-inhabiting arthropods. We need much more information on food chains, and interrelationships between soil organisms, before we can understand the overall contribution of macroarthropods to litter breakdown.

TABLE VI. Approximate consumption of litter by macroarthropods (g m^{-2})

Average deciduous litter fall	3000
Isopoda	73
Symphyla	60
Diplopoda	146
Isoptera	570[a]
Diptera and Coleoptera	180

[a] Maldague (1964).

References

ADAMSON, A. M. (1943). *Trop. Agric., Trin.* **20,** 107–112.

D'AGUILAR, J. and BESSARD, A. (1963). *In* "Soil Organisms." (J. Doeksen and J. van der Drift, eds), pp. 103–108. North-Holland, Amsterdam.

BLOWER, J. G. (1956). "*6th Congr. Sci. du Sol. Paris,*" 169–175.

BOCOCK, K. L. (1963). *In* "Soil Organisms." (J. Doeksen and J. van der Drift, eds), pp. 85–91. North-Holland, Amsterdam.

BORNEBUSCH, C. H. (1930). *Forstl. Forsogsvaesens Meddel. Bereta, Copenhagen* **96,** 1–225.

BRAY, J. R. and GORHAM, E. (1964). *Adv. ecol. Res.* **2,** 101–157.

CLOUDSLEY-THOMPSON, J. L. (1951). *Proc. Zool. Soc. Lond.* **121,** 253–277.

DRIFT, J. VAN DER (1951). *In* "Experimental Pedology." (E. G. Hallsworth and D. V. Crawford, eds), pp. 227–235.

DUNGER, W. (1958). *Zool. Jb.* (*Syst.*) **86,** 139–180.

DUNGER, M. (1962). *Proc. 11th Int. Congr. Ent.* Wien 1960 **3,** 169.

EATON, T. H. Jr. (1943). *Am. Midl. Nat.* **29,** 713–723.

EDWARDS, C. A. (1958). *Ent. exp. appl.* **1,** 308–319.

EDWARDS, C. A. (1961). *Ent. exp. appl.* **4,** 239–256.

EDWARDS, C. A. (1967). *In* "Progress in Soil Biology." (O. Graff and J. E. Satchell, eds), pp. 585–594. North-Holland, Amsterdam.

EDWARDS, C. A. and HEATH, G. W. (1963). *In* "Soil Organisms." (J. Doeksen and J. van der Drift, eds), pp. 76–84. North-Holland, Amsterdam. (1974). *Pedobiologia*, in press.

EDWARDS, C. A., REICHLE, D. E. and CROSSLEY, D. A. (1970). *In* "Ecological Studies, Analysis and Synthesis." (D. E. Reichle, ed.), Vol. 1, pp. 147–172. Springer-Verlag, Berlin.

FRANZ, H. and LEITENBERGER, L. (1948). *Öst. zool. Z.* **1**, 498–518.

GERE, G. (1957). *Acta Biol.* (Budapest) **7**, 257–271.

HARRIS, W. V. (1955). *In* "Soil Zoology." (D. K. McE. Kevan, ed.), pp. 62–72. Butterworths, London.

HEATH, G. W. and KING, H. G. C. (1964). *Proc. 8th Int. Cong. Soil Sci.* Bucharest, 779–986.

HUNGATE, R. E. (1943). *Ann. ent. Soc. Am.* **36**, 730–739.

HUBBELL, S. P., SIKOVA, A. and PARIS, O. H. (1965). *Health Physics* **11**, 1485–1501.

JACOT, A. P. (1940). *Q. Rev. Biol.* **15**, 28–58.

KALSHOVEN, L. G. E. (1941). *Tectona* **34**, 568–582.

KARPACHEVSKY, L. O., PEREL, T. S. and BARTSEVICH, V. V. (1968). *Pedobiologia* **8**, 146–149.

KEVAN, D. K. MCE. (1962). "Soil Animals." H. F. and G. Witherby, London.

KING, H. G. C. and HEATH, G. W. (1967). *Pedobiologia* **7**, 192–197.

KUBIENA, W. L. (1955). *In* "Soil Zoology." (D. K. McE. Kevan, ed.), pp. 73–82. Butterworths, London.

KÜHNELT, W. (1961). "Soil Biology." Faber and Faber, London.

KURCHEVA, G. F. (1960). *Pochvovedenie* **4**, 16–23.

LEE, K. E. and WOOD, T. G. (1971). "Termites and Soils." Academic Press, London and New York.

LYFORD, W. H. Jr. (1943). *Ecology* **24**, 252–261.

MALDAGUE, M. E. (1964). *Proc. 8th Int. Cong. Soil Sci.* Bucharest, Vol. 3, 743–755.

MARCUZZI, G. (1970). *Pedobiologia* **10**, 401–406.

NEF, L. (1957). *Agricultura* (Louvain) **5**, 245–366.

NIELSEN, C. O. (1962). *Oikos* **13**, 200–215.

O'NEILL, R. V. (1968). *Ecology* **49**, 803–809.

PEREL, T. S., KARPACHEVSKY, L. O. and YEGOROVA, E. V. (1971). *Pedobiologia* **11**, 66–70.

PHILLIPSON, J. (1966). *Proc. Symp. on Terrestrial Secondary Production*, Warsaw, 459–473.

SAITO, S. (1965). *Jap. J. Ecol.* **15**, 47–55.

SAITO, S. (1970). *In* "Methods of Study in Soil Ecology." (J. Phillipson, ed.), pp. 215–223. UNESCO, Paris.

SATCHELL, J. E. and LOWE, D. G. (1967). *In* "Progress in Soil Biology." (O. Graff and J. E. Satchell, eds), pp. 102–120. North-Holland, Amsterdam.

SEIFERT, K. (1962). *Holzforschung* **19**, 105–111.

SHAW, G. G. (1968). *Ecology* **49**, 1163–1166.

SHAW, G. G. (1970). *Pedobiologia* **10**, 389–400.

STRICKLAND, A. H. (1944). *Trop. Agric., Trin.* **21**, 107–114.

STRICKLAND, A. H. (1945). *J. Anim. Ecol.* **14**, 1–11.

STRIGANOVA, B. R. (1971). *In* "Organismes du Sol et Production Primaire 4th Colloquium Pedobiologiae Dijon." Institut National de la Recherche Agronomique, Paris.

SUTTON, S. L. (1972). "Woodlice." Ginn and Company, Limited, London.

SZABO, J., BARTFAY, T. and MARTON, M. (1966). *In* "Progress in Soil Biology." (O. Graff and J. E. Satchell, eds), pp. 475–489. North-Holland, Amsterdam.

THIELE, H. U. (1956). *Z. angew. Ent.* **39,** 316–367.

WILLIAMS, E. C. (1941). *Bull. Chicago Acad. Sci.* **6,** 63–124.

ZACHARIAE, G. (1965). *Forst. wiss Forschungen Hamburg* **20,** 1–68.